A new mosasaur from the Late Cretaceous of Nigeria

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ABSTRACT

The Late Cretaceous of Africa has produced a diverse fauna of mosasaurs, including the highly specialized, long-jawed *Pluridens*. The type of *Pluridens walkeri* comes from the Maastrichtian aged Farin-Doutchi formation of Niger, while a second, referred specimen was reported from the Campanian aged Nkporo Shale near Calabar, in southern Nigeria. Comparisons of this referred specimen with the holotype suggest that it represents a distinct and more primitive species of *Pluridens*. The Calabar jaw resembles *P. walkeri* in being long and narrow anteriorly with a shallow subdental shelf, and in having small, numerous, recurved teeth with medially positioned replacement pits. However, it lacks many of the derived features that characterize *Pluridens walkeri*, such as the extremely long and straight jaw, the extreme lateral protrusion and subcircular section of the dentary, strong transverse expansion of the dental thecae, and extreme reduction and increase in number of the teeth. The Calabar *Pluridens* is therefore referred to a new species, *Pluridens calabaria*. Following recent studies, *Pluridens* is considered to represent a highly derived member of the Halisaurinae. The marked differences between the Campanian and Maastrichtian species of the genus underscore the rapid pace of mosasaur evolution during the Cretaceous.

Keywords:
Squamata
Mosasauridae
Halisaurinae
Pluridens
Africa

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1. Introduction

The Mosasauridae is a family of highly specialized marine lizards known from the Late Cretaceous period (Polcyn et al., 2013). Mosasaurids are related to (Carroll and Debraga, 1992; Gauthier et al., 2012) or perhaps derived from (Polcyn et al., 2013)(Bell and Polcyn, 2005) the "aigialosaurs", small marine lizards that thrived in the

Cenomanian and Turonian. In the Turonian, the mosasaurids appeared and underwent a major radiation (Polcyn et al., 2013). The adaptive radiation of mosasaurs was associated with increased specialization for a marine lifestyle, evolution of increased body size in a range of lineages, and evolution of a diverse range of jaw and tooth morphologies to exploit a range of feeding styles (Polcyn et al., 2013). By the end of the Cretaceous, mosasaurs had adapted to produce piscivores, durophages, and apex predators capable of preying on large fish and other marine reptiles- including other mosasaurs (Bell Jr and Barnes, 2007; Everhart, 2008).

Mosasaurs were global in their distribution, but the group appears to have been especially diverse in the shallow seas that surrounded Africa. Although African mosasaur assemblages are neither as thoroughly explored nor as well studied as the European and North American assemblages, they have never the less produced a remarkably rich fauna (Lingham-Soliar, 1991; Schulp et al., 2008; Schulp et al., 2009; Bardet et al., 2010; Polcyn et al., 2010; Leblanc et al., 2012; Mateus et al., 2012; Bardet et al., 2015).

Among these are the mosasaurs from Niger and Nigeria (Soliar, 1988; Lingham-Soliar, 1991, 1998). Previous studies of the mosasaur fauna of the Maastrichtian aged Farin-Doutchi Formation of Niger have revealed a high diversity of species. Familiar taxa include halisaurines, plioplatecarpines, tylosaurines, and mosasaurines (Soliar, 1988; Lingham-Soliar, 1991). However, two highly specialized mosasaurs of uncertain affinities are present as well. The first is *Goronyosaurus nigeriensis* (Soliar, 1988). It is unusual in having long jaws with large, interlocking, spike-like teeth. The second is *Pluridens walkeri* (Lingham-Soliar, 1998). *Pluridens* is characterized by an extremely elongate mandible and a large number of small, recurved teeth.

Only a single specimen of *Pluridens walkeri* was recovered from the Farin-Doutchi formation (Lingham-Soliar, 1998). However a similar specimen was recovered from the Nkporo Formation in southern Nigeria near the city of Calabar (Lingham-Soliar, 1998). In the original description, this specimen was referred to *Pluridens walkeri*. However, it differs markedly from the holotype in its morphology and comes from an older, late Campanian aged horizon. Here, this specimen is shown to represent a new species.

2. Geological Setting

According to notes with the fossil, the specimen was collected in southern Nigeria (Fig. 1) from the upper Campanian-lower Maastrichtian Nkporo Shale (Fig. 2). The specimen was collected along the Ekpena Road, at the 36 km milepost, which would put it in the very base of the Nkporo Shale, in the zone of *Sphenodiscus lobatus* and *Libycoceras afikpoense* (Zaborski, 1982). These ammonites are thought to be Late Campanian in age, and have specifically been correlated with the *Nostocera* (*Bostrychoceras*) *polyplocum* ammonite zone (Zaborski, 1985) of Europe. The *polyplocum* zone extends from roughly 74.6-75.5 Ma (Voigt et al., 2012).

3. Systematic Paleontology

Reptilia Laurenti, 1768
Squamata Oppel, 1811
Mosasauroidea Gervais 1853
Mosasauridae Gervais 1853
Halisaurinae Bardet and Peredo-Superbiola 2005
Pluridens Lingham-Soliar 1998

Emended diagnosis. Medium-sized mosasaur exhibiting the following combination of characters: dentaries elongate and slender anteriorly, dentary bulging laterally to project well beyond toothrow in dorsal view and giving the anterior end of the mandible a cylindrical cross section; subdental shelf dorsoventrally narrow in medial view, and with ventral lip of dentary strongly expanded to constrict Meckelian groove anteriorly. Teeth small and numerous (25-30 or more); with tooth replacement pit located medially rather than posteromedially, tooth sockets moderately to strongly transversely expanded. Tooth crowns short and strongly hooked, with enamel bearing very fine sculpture of anastomosing ridges. Tooth roots posteriorly inclined in medial view; interdental ridges prominent and inclined posteriorly in medial view.

Type species. *Pluridens walkeri*

Pluridens walkeri Lingham-Soliar 1998

Emended diagnosis. *Pluridens* with extremely long, slender jaw. Dorsal margin of jaw weakly concave in lateral view. Tooth row strongly bowed medially in dorsal view. Jaw with a strongly rounded cross-section anteriorly and very strong lateral bulge, with lateral margin protruding far beyond tooth row in dorsal view; ~30 small closely-packed teeth, with tooth sockets anteroposteriorly narrow and strongly expanded mediolaterally.

Holotype. BMNH R14153, right dentary (Fig. 3)

Horizon and Locality. Igdaman locality, Early Maastrichtian aged (Collins and Ward, 2010) Farin-Doutchi Formation, northern Nigeria.

Pluridens calabaria sp. nov.

Etymology. In reference to the city of Calabar, near the type locality.

Diagnosis. Small *Pluridens*; jaw slender anteriorly but dorsoventrally expanded posteriorly with a strongly concave dorsal margin; toothrow weakly curved in dorsal view. Lateral bulge of dentary weakly developed compared to *P. walkeri*. Teeth ~25 (estimated); teeth larger and tooth bases less anteroposteriorly compressed than in *P.*

walkeri, dental thecae only weakly expanded transversely. Interdental plates and tooth bases inclined posteriorly in medial view.

Holotype. BMNH R9804, partial right dentary and associated splenial (Fig. 4).

Horizon and Locality. Middle Campanian Nkporo Shale, *Nostocera* (*Bostrychocera) polyplocum* ammonite zone, near Calabar, southern Nigeria.

Description. BMNH R9804 consists of the middle part of a right dentary, along with the associated splenial, and a tooth that has fallen out of the jaw.

The dentary is low and has an elliptical cross section anteriorly, then rapidly becomes deeper posteriorly, until it is about 2.5 times the anterior depth of the jaw. A similar jaw shape- tapered anteriorly, but flared posteriorly- is seen in *P. walkeri*, but the posterior expansion is more extreme here. Although the jaw is incomplete, the strong posterior expansion of the jaw indicates that the dentary did not have the very long, low profile seen in *P. walkeri*.

In dorsal view, the dentary is distinctly bulged outward in dorsal view. A similar feature is seen in *P. walkeri*, but developed to a greater extreme in that taxon, where the lateral wall of the dentary both projects laterally to a greater degree, and this lateral expansion is extended anteriorly and posterior relative to the condition in *P. calabaria*. The toothrow is weakly bowed in dorsal view, rather than strongly bowed as in *P. walkeri*.

Anteriorly, the ventral margin of the jaw wraps up around the Meckelian canal to constrict the Meckelian canal; again the same character is seen in *P. walkeri*. This feature is developed to varying degrees in other mosasaurs, notably *Halisaurus arambourgi* (Bardet et al., 2005) but not to the same degree as seen in *Pluridens*.

A subdental ridge (= subdental lamina) bounds the teeth medially. The subdental ridge is dorsally expanded into a prominent subdental shelf that obscures the bases of the teeth in lateral view. This is a derived feature seen in other mosasaurids, but the subdental ridge is shallow compared to the condition seen in more derived mosasaurs. A similar condition is seen in *Pluridens walkeri* (Lingham-Soliar, 1998); this feature could either represent a plesiomorphy, or a derived character uniting the two, depending on its polarity. Unlike many mosasaurs, the subdental shelf does not extend up as far as dental parapet, but lies below the lateral parapet of the jaw such that the tooth bases are partly exposed; this is likely to represent the primitive condition.

14 tooth positions are preserved, but additional teeth would have been present anteriorly and posteriorly. The total number of teeth is estimated to be around 25, more than in most mosasaurs but less than *Pluridens walkeri*.

Teeth implant into sockets, with the alveolar groove formed by the lateral parapet and subdental ridge being divided into sockets by interdental ridges formed of alveolar bone (Caldwell et al., 2003). As in *P. walkeri*, teeth are closely packed. Thecae are slightly wider than tall in dorsal view, but not laterally expanded to the degree seen in *P. walkeri*. A similar condition is seen the halisaur *Eonatator* from the Selma Formation of Alabama (Lindgren and Siverson, 2005).

The interdental ridges separating the teeth are difficult to see because most sockets are either damaged or contain an attached tooth. However, the interdental ridges

appear to be well-developed and project above the subdental shelf, as in *P. walkeri* (Fig. 4). In medial view, the subdental ridges are inclined posteriorly, as in *P. walkeri* (Fig. 4), an autapomorphy of the genus.

Tooth crowns are broken off of all the attached teeth, but an isolated tooth is preserved (Fig. 5). The crown is relatively short; although the tip is broken, the complete tooth would be only slightly taller than the anteroposterior width of the base; a similar short tooth crown is seen in *P. walkeri* (Fig. 3). The tooth crown is mediolaterally compressed, with an elliptical cross section. A carina is present on the anterior margin, but the posterior margin is damaged and so it is unclear if a carina was present (Figs. 5,6). The surface of the tooth is covered with a series of fine, closely packed, wavy striae. A similar sculpturing is seen in the Selma *Eonatator* (Lindgren and Siverson, 2005).

The tooth base is formed of a massive, swollen pedicel (Fig. 5) formed of cementum (Caldwell et al., 2003), as in other mosasaurids. In contrast to *P. walkeri*, the tooth roots are subcircular, not mediolaterally expanded. The tooth root is distinctly inclined, such that the tooth root slants posteriorly in medial view, as in *P. walkeri*. This inclined tooth root is associated with the distinct posterior inclination of the interdental ridges, and represents a derived character of the genus.

4. Discussion.

Affinities of the Calabar jaw. A number of features support a close relationship between *Pluridens walkeri* and the Nkporo mosasaur. The dentaries share the following characters: the dentary is long and narrow anteriorly; the subdental shelf is shallow, and the Meckelian groove is constricted anteriorly by a prominent ventral lip of the dentary. The teeth are also similar in being small, short, and strongly hooked. Furthermore, both show a derived form of tooth replacement, where interdental pits develop medially rather than posteromedially as in other mosasaurs. Finally, both have tooth roots and interdental ridges that are posteriorly inclined. Based on these synapomorphies, the Nkporo jaw can be assigned to *Pluridens*.

Pluridens walkeri exhibits numerous derived characters that are absent in the Nkporo specimen, however. The dentary of *P. walkeri* appears to have been overall more elongate, and distinctly bulges laterally out beyond the toothrow such that the anterior dentary has a cylindrical cross section. The teeth are also smaller and more numerous (~30 vs. ~25), and the dental thecae and tooth roots are unique among mosasaurs in being strongly mediolaterally expanded. These features are unlikely to result from ontogeny: large samples of *Platecarpus* from the chalks of Kansas, for example, do not show similar levels of variation between individuals (pers. obs. of YPM and AMNH collections). Instead, the marked variation between the two suggests that they are distinct taxa. Neither do the differences appear to be taphonomic, both jaws appear to be three-dimensionally preserved and undistorted.

Pluridens is highly derived relative to other mosasaurs. Its affinities have therefore been unclear (Lingham-Soliar, 1998), and Lingham-Soliar went so far as to suggest that the animal might deserve its own subfamily. However there are a number of characters of the jaws and teeth that could potentially shed light on its affinities. For

example, the long and slender dentary and the high tooth count are shared with *Halisaurus arambourgi* (Bardet et al., 2005) and *Eonatator* (Lindgren and Siverson, 2005). *Halisaurus arambourgi* is also characterized by a prominent ventral lip of the dentary below the Meckelian groove (Bardet et al., 2005), as in *Pluridens*. *Halisaurus platyspondylus* differs from *Pluridens* in having subcircular dental alveoli and posteromedially positioned replacement pits, but *Eonatator* is similar to *Pluridens* in terms of having transversely expanded alveoli with medially positioned replacement pits (Lindgren and Siverson 2005: Fig 3.2); the teeth also exhibit a similar form of finely striated sculpturing (Lindgren and Siverson, 2005). All of these features suggest that *Pluridens* is most likely a large and highly derived member of the Halisaurinae.

The similarities between *Pluridens* and halisaurs have previously been noted (Lindgren and Siverson, 2005) and on this basis it was argued that *Pluridens* represented a junior synonym of *Halisaurus* (Lindgren and Siverson, 2005). There is no objective, scientific criterion for determining how different two species must be to qualify for generic distinction, but in the authors opinion, the highly derived jaw morphology of *Pluridens* would seem to warrant a separate genus for *P. walkeri* and *P. calabaria*.

Biostratigraphy. The two *Pluridens* are separated by several million years. The Farin-Doutchi Formation is Maastrichtian in age based on faunal correlations (Lingham-Soliar, 1998), probably Early Maastrichtian (Collins and Ward, 2010), making it no older than 72.1 Ma (Gradstein et al., 2012). The Nkporo Shale spans the Upper Campanian and the lower Maastrichtian (Lingham-Soliar, 1998) however the type of *P. calabaria* is reported as coming from the basal part of the Nkporo that is correlated with the *polyplocum* ammonite zone(Zaborski, 1982, 1985). The *polyplocum* zone has recently been correlated to a narrow interval that begins at approximately 75.5 Ma, during the Late Campanian Event (LCE) and extends until approximately 74.6 Ma. (Voigt et al., 2012). This makes *P. calabaria* anywhere from 2.5 to 6.5 million years older than *P. walkeri*, depending on the precise age of the Farin-Doutchi Formation. Given this, it is hardly surprising to find that the two represent separate species.

That different species should be found in sediments of different ages is perhaps unsurprising. Mosasaurs show a dramatic radiation in the Late Cretaceous, rapidly evolving large, highly specialized forms occupying a remarkable range of niches over a span of around 30 million years (Polcyn et al., 2013). Evidence from both fossils and molecules suggests that squamates in general evolve rapidly. In North America, Late Cretaceous lizards show relatively rapid turnover, with distinct species found in the Campanian (Gao and Fox, 1996; Nydam and Voci, 2007) and Maastrichtian (Estes, 1964; Gao and Fox, 1996; Longrich et al., 2012). Similarly, the high diversity of extant squamates implies that the clade as a whole is characterized by rapid rates of speciation. Today, there are almost 10,000 extant species (Uetz and Hošek, 2014) with most of the diversity accumulating since the end of the Cretaceous (Longrich et al., 2012).

Rapid evolution may characterize Cretaceous biotas in general. High rates of turnover are seen within nannoplankton (Sissingh, 1977) and ammonites (Kent and Gradstein, 1985) in marine ecosystems, and among dinosaurs (Mallon et al., 2012) mammals (Kielan-Jaworowska et al., 2004) and angiosperms (Braman and Sweet, 2012) in terrestrial ecosystems. Such high rates of turnover suggest that mosasaurs (like many other species) are likely to be short-lived. This does not justify creating

new species based solely based on differences in age, but it does provide a strong hint that we should look for differences between mosasaurs found at different time periods, and not be surprised when we find them.

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Figures

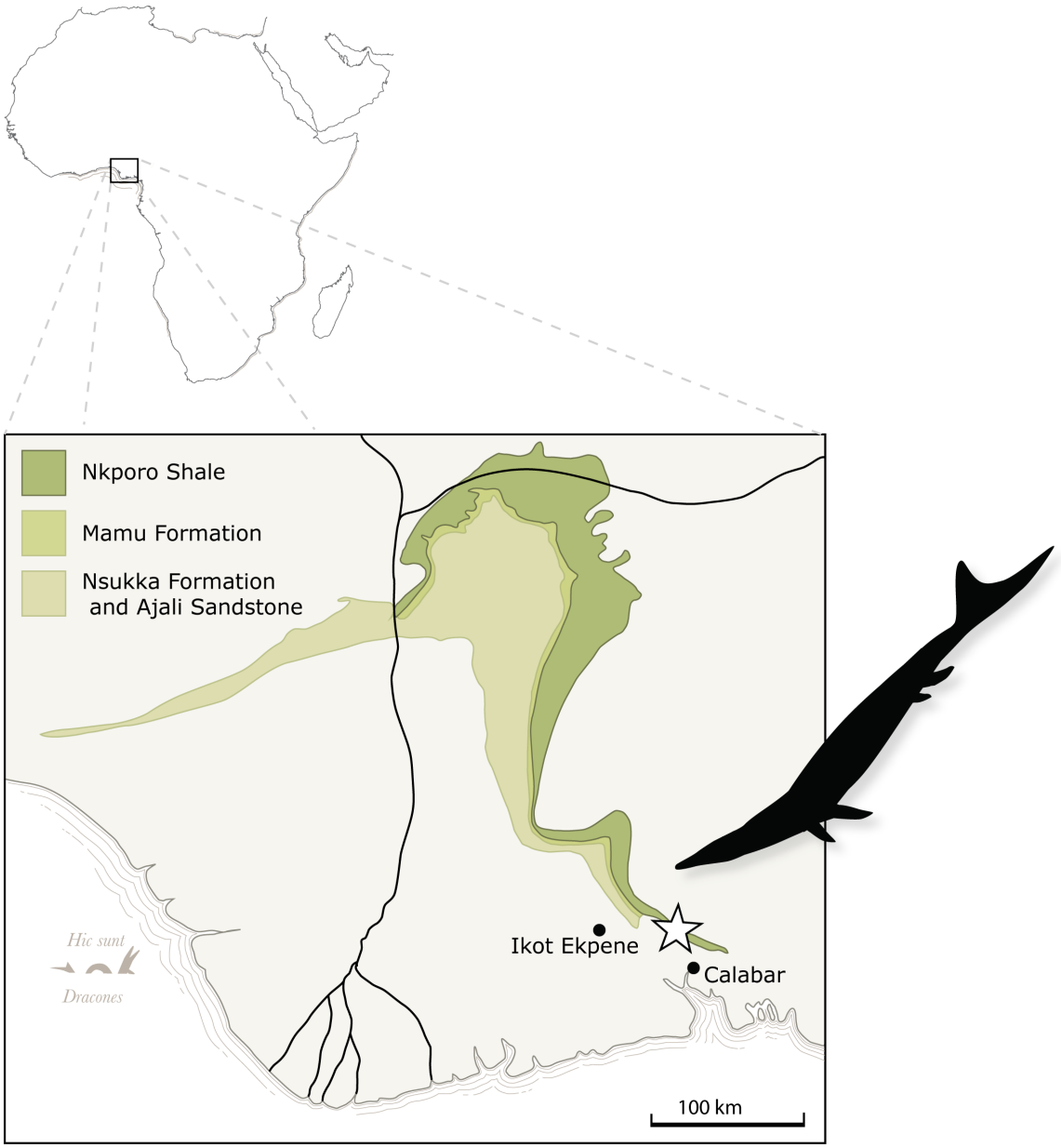

Fig. 1. Map showing the location of the site that produced the holotype of *Pluridens calabaria*. Map redrawn from Zaborski (Zaborski, 1982). The specimen was collected along the road between Calabar and Ikot Ekpene, near milepost 36.

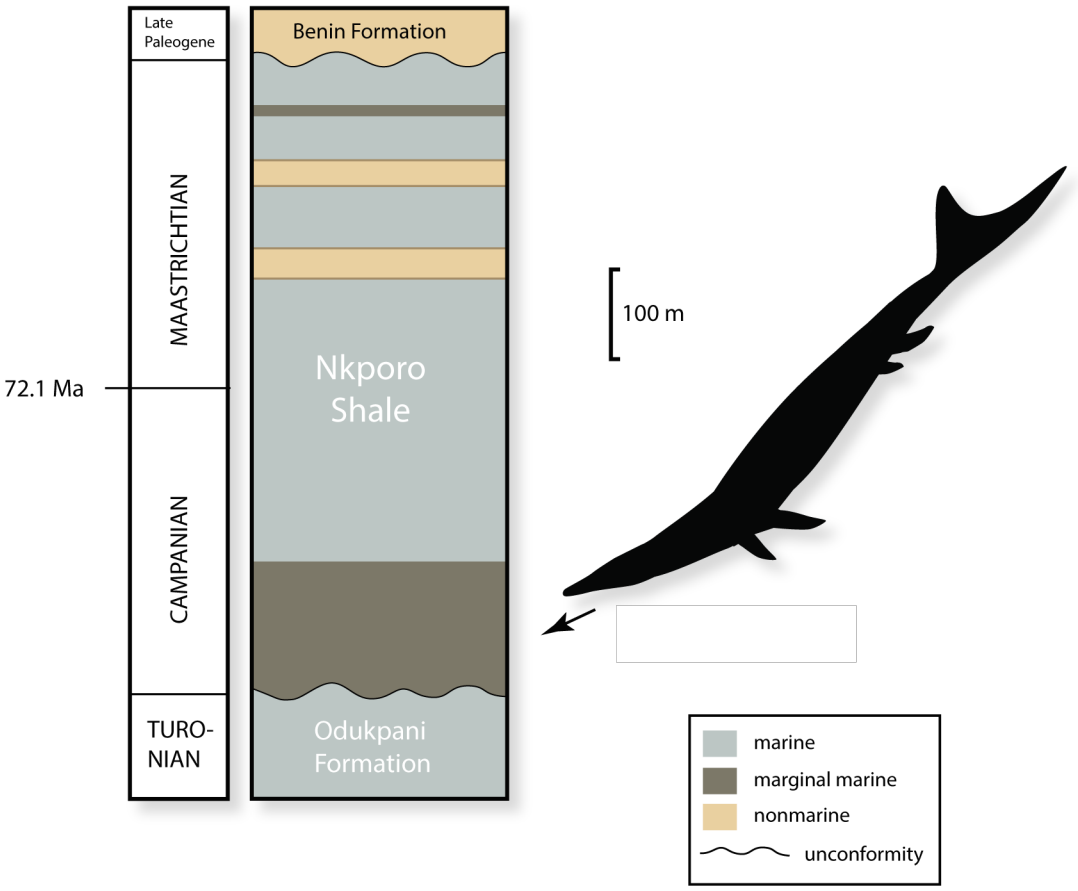

Fig. 2. Stratigraphic column of the upper Campanian-lower Maastrichtian Nkporo Shale exposures between Calabar and Ikot Ekpene, showing the stratigraphic position of *Pluridens calabaria*. *Pluridens* lies relatively low in the Nkporo Shale, in the *Nostocera* (*Bostrychocera) polyplocum* ammonite zone. Stratigraphic column redrawn from Zaborski (Zaborski, 1982).

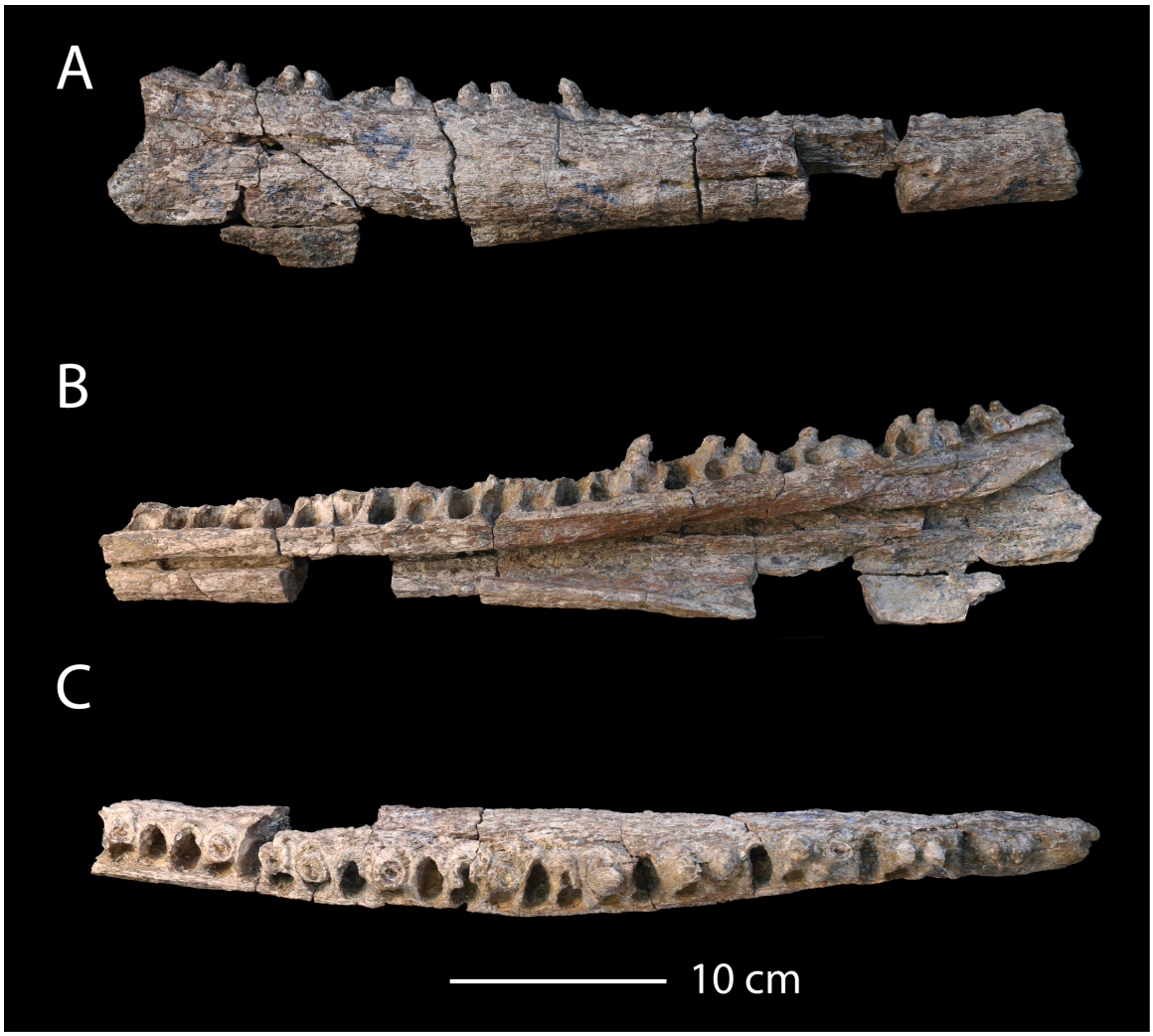

Figure 3. *Pluridens walkeri* from the Maastrichtian Farin-Doutchi Formation of northern Nigeria, BMNH R14153, holotype right dentary. **A**, lateral view; **B**, medial view; **C**, dorsal view.

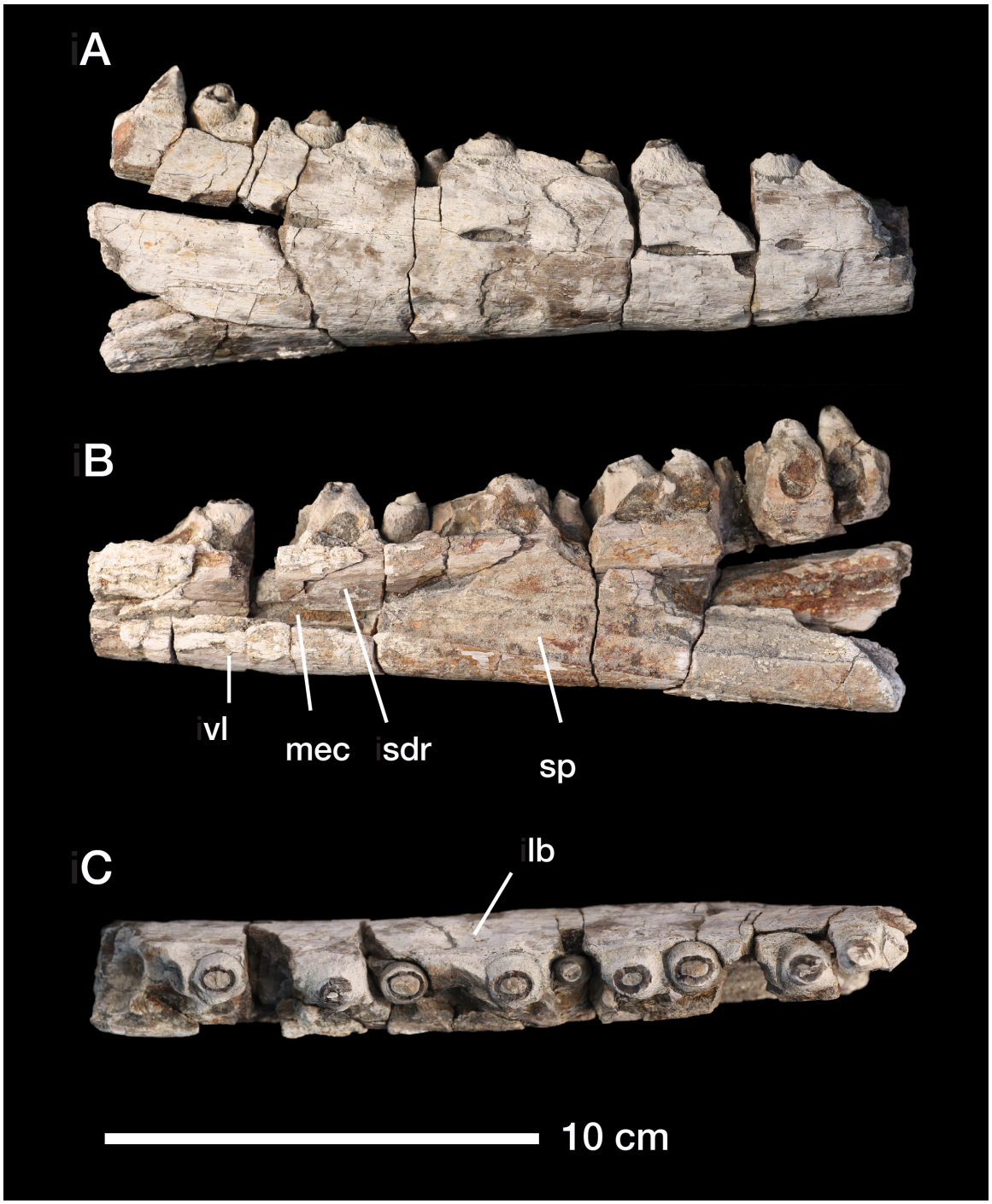

Figure 4. *Pluridens calabaria* n. sp. from the Campanian Nkporo Shale, southern Nigeria, BMNH R9804, holotype right mandible. **A**, lateral view; **B**, medial view; **C**, dorsal view. Abbreviations: lb, lateral buttress, mec, Meckelian canal, sdr, subdental ridge, sp, splenial, vl, ventral lip;

Fig. 5. *Pluridens calabaria* n. sp., BMNH R9804, isolated tooth. **A**, medial view, **B**, lateral view, **C**, posterior view, **D**, anterior view.

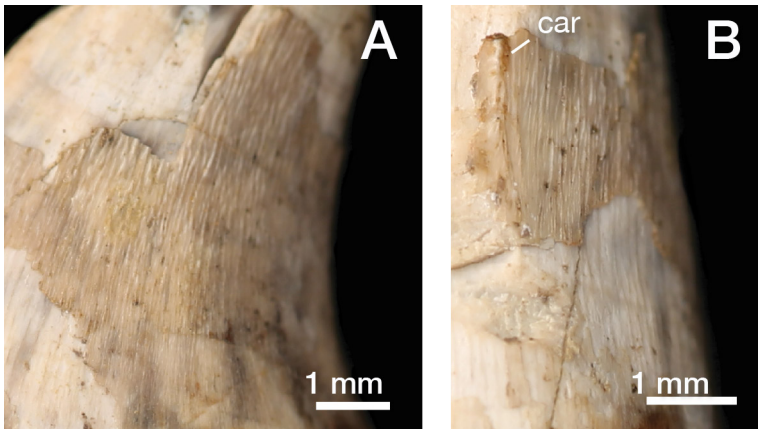

Fig. 6. *Pluridens calabaria* n. sp., BMNH R9804, isolated tooth. **A**, medial view, **B**, anterior view.

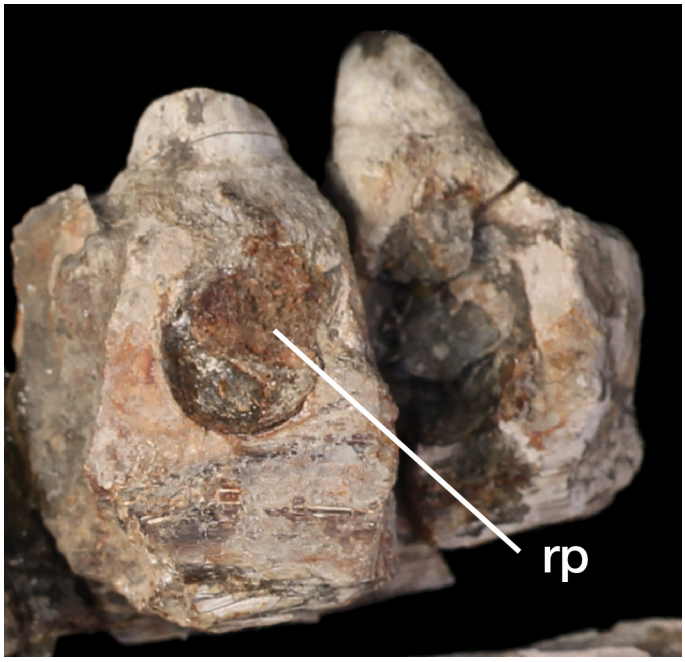

Fig. 7. *Pluridens calabaria* n. sp., BMNH R9804, showing characteristic medially placed replacement pits (second preserved tooth from back of dentary). Abbreviations: rp, replacement pit.

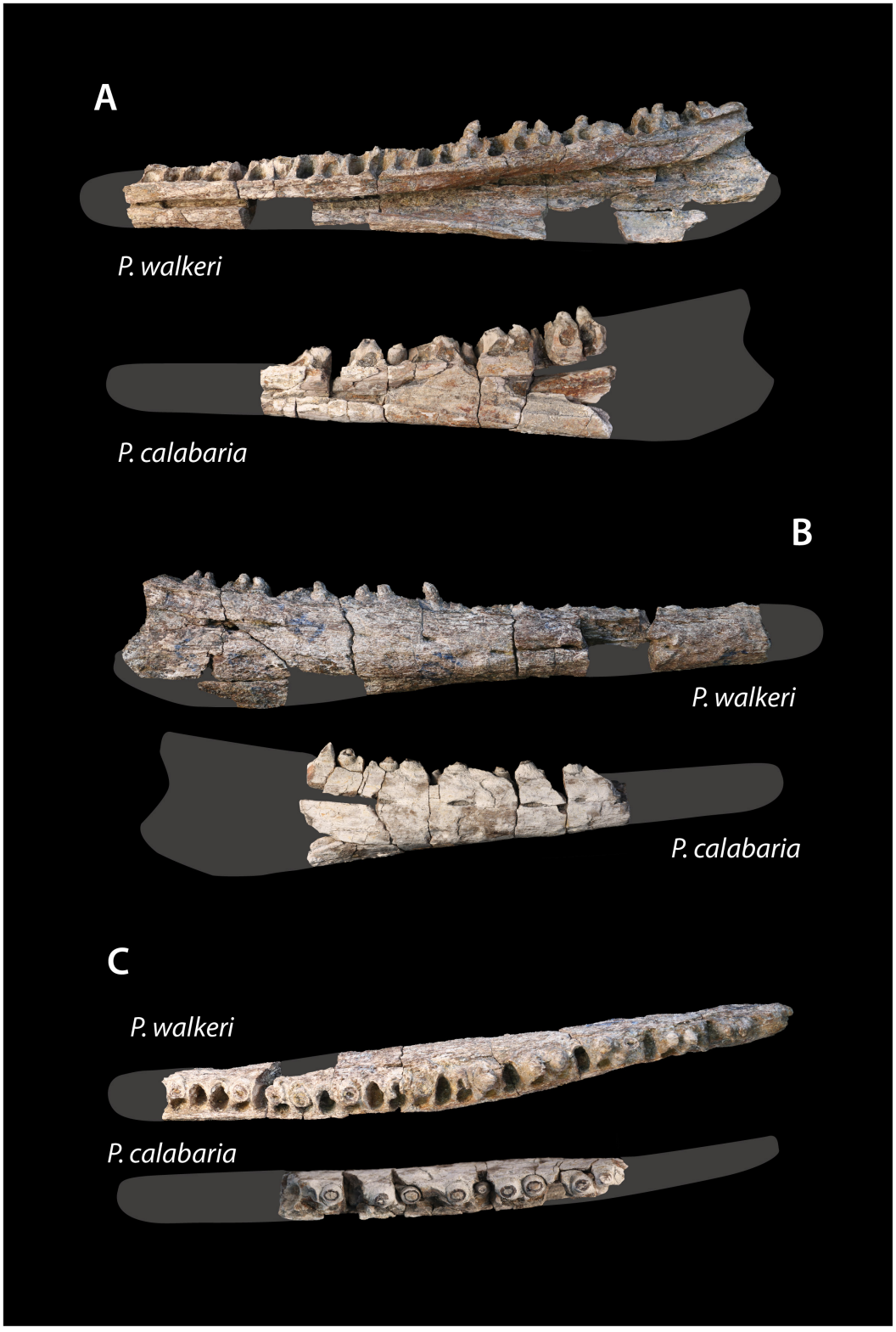

Fig. 8. *Pluridens calabaria* versus *P. walkeri*. **A**, medial, **B**, lateral, **C**, dorsal view.